

1-1-2015

# Liana Competition with Tropical Trees Varies Seasonally but not with Tree Species Identity

Leonor Álvarez-Cansino  
*University of Wisconsin - Milwaukee*

Stefan A. Schnitzer  
*Marquette University, stefan.schnitzer@marquette.edu*

Joseph P. Reid  
*University of Minnesota - Twin Cities*

Jennifer S. Powers  
*University of Minnesota*

# Liana competition with tropical trees varies seasonally but not with tree species identity

LEONOR ÁLVAREZ-CANSINO,<sup>1,2,4</sup> STEFAN A. SCHNITZER,<sup>1,2</sup> JOSEPH P. REID,<sup>3</sup> AND JENNIFER S. POWERS<sup>2,3</sup>

<sup>1</sup>University of Wisconsin School of Freshwater Sciences, P.O. Box 413, Milwaukee, Wisconsin 53201 USA

<sup>2</sup>Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panama

<sup>3</sup>University of Minnesota, Departments of Ecology, Evolution, and Behavior and Plant Biology, 1987 Upper Buford Circle, Saint Paul, Minnesota 55108 USA

**Abstract.** Lianas in tropical forests compete intensely with trees for above- and belowground resources and limit tree growth and regeneration. Liana competition with adult canopy trees may be particularly strong, and, if lianas compete more intensely with some tree species than others, they may influence tree species composition. We performed the first systematic, large-scale liana removal experiment to assess the competitive effects of lianas on multiple tropical tree species by measuring sap velocity and growth in a lowland tropical forest in Panama. Tree sap velocity increased 60% soon after liana removal compared to control trees, and tree diameter growth increased 25% after one year. Although tree species varied in their response to lianas, this variation was not significant, suggesting that lianas competed similarly with all tree species examined. The effect of lianas on tree sap velocity was particularly strong during the dry season, when soil moisture was low, suggesting that lianas compete intensely with trees for water. Under the predicted global change scenario of increased temperature and drought intensity, competition from lianas may become more prevalent in seasonal tropical forests, which, according to our data, should have a negative effect on most tropical tree species.

**Key words:** Barro Colorado National Monument, Panama; competition; competitive effects; liana removal; sap velocity; tree growth; tropical forest.

## INTRODUCTION

Lianas are important components of tropical forests, where they commonly comprise 25% of the number of woody stems and species (Schnitzer and Bongers 2002). Evidence is accruing that lianas compete intensely with co-occurring trees, reducing tree regeneration, growth, fecundity, survival, and diversity (Pérez-Salicrup 2001, Ingwell et al. 2010, Schnitzer and Carson 2010). Liana infestation of trees is increasingly common, and lianas can compete with >75% of the trees in many tropical forests (Ingwell et al. 2010, van der Heijden et al. 2013). Lianas compete with trees by deploying their branches and leaves above those of their host trees, where they directly reduce light availability, as well as exert mechanical damage that can induce changes in tree leaf and branch area index (Schnitzer and Bongers 2002, Sánchez-Azofeifa et al. 2009). Lianas may also compete with trees for belowground resources, particularly water (Schnitzer et al. 2005, Toledo-Aceves and Swaine 2008). Liana competition with trees may be particularly intense for soil water during the dry season because, as soil

moisture becomes limiting, many liana species continue to grow substantially more than co-occurring trees, and the latter appear to suffer more from limiting soil moisture (Schnitzer 2005, Toledo-Aceves and Swaine 2008, Cai et al. 2009). Few experimental studies, however, have compared the seasonal variation in liana competition with trees, and fewer yet have experimentally examined the effects of lianas on adult trees (e.g., Pérez-Salicrup and Barker 2000, Tobin et al. 2012).

Tree species may differ markedly in their response to liana competition. Several studies have now demonstrated that lianas have a greater effect on slow-growing, shade-tolerant trees with high wood density than on some fast-growing pioneer trees, such as *Cecropia* (Clark and Clark 1990, van der Heijden et al. 2008, Ingwell et al. 2010, Schnitzer and Carson 2010). However, it is not clear whether the effects of lianas vary among shade-tolerant tree species, which comprise the vast majority of the tree community. Furthermore, liana abundance is now increasing relative to trees in many Neotropical forests (Schnitzer and Bongers 2011), and thus, if shade-tolerant tree species vary in their response to liana competition, increasing lianas could influence tree community composition and tree species' relative abundances (Schnitzer et al. 2011).

We used an experimental approach to quantify the effect of lianas on tree sap velocity, the seasonal effect of lianas on soil water availability and tree sap velocity,

Manuscript received 28 May 2014; revised 18 September 2014; accepted 24 September 2014. Corresponding Editor: T. P. Young.

<sup>4</sup> Present address: Department of Plant Ecology, University of Bayreuth, Universitätsstrasse 30, 95440 Germany.  
E-mail: lalvarezcansino@gmail.com

and whether tree species differ in their response to the presence of lianas. This is the first study to test whether seasonal tree physiological and growth responses to liana competition vary among tree species within a community. We conducted our study on seven largely shade-tolerant tree species in the context of a large-scale liana removal experiment in the Barro Colorado National Monument, Panama (BCNM). We tested three main hypotheses: (1) Lianas compete with trees, thus reducing tree physiological performance and growth, (2) liana competition is strongest during seasonal drought, and (3) the strength of liana competition varies with tree species identity. We used the relative change in tree sap velocity before and after liana cutting in liana removal and control plots as an indicator of physiological performance. We used tree diameter growth for one year after liana cutting to examine the longer term effects of liana competition.

## METHODS

### *Experimental design and study species*

We conducted the study in a secondary (~55 year-old) semi-deciduous tropical moist forest on Gigante Peninsula, a mainland portion of the BCNM. Mean annual temperature and precipitation of Gigante Peninsula are 27°C and 2600 mm, respectively, with a four-month dry season from mid-December to April that contributes <10% of the annual precipitation (Leigh 1999). Liana density on Gigante Peninsula is ~2000 rooted stems/ha ( $\geq 1$  cm diameter; S. A. Schnitzer, *unpublished data*), which is moderate compared to some tropical forests (Pérez-Salicrup et al. 2001; see Plate 1).

In 2008, we established 16  $80 \times 80$  m plots that were similar with respect to slope and liana abundance. The plots were large enough to contain the stems and crowns of multiple large trees and lianas, and the mean density of trees  $\geq 1$  cm diameter at breast height (dbh) was ~3600 trees/ha (S. A. Schnitzer, *unpublished data*). In each plot, we tagged, measured the stem diameter (1.3 m from the roots), mapped the rooting location, and identified to species all lianas and trees  $\geq 1$  cm diameter in the central  $60 \times 60$  m, as well as all trees  $\geq 20$  cm dbh and lianas  $\geq 5$  cm diameter in the entire  $80 \times 80$  m plot. We followed explicitly the census methods developed for lianas by Gerwing et al. (2006) and Schnitzer et al. (2008), and for trees by Condit (1998).

In April 2011, late in the dry season, we cut lianas near the soil surface in the entire  $80 \times 80$  m plot of eight randomly assigned plots, leaving the remaining eight plots as unmanipulated controls. To avoid damaging the trees, we did not remove liana crowns and stems because they are commonly entangled in the tree crowns. Instead, we allowed the lianas to defoliate and decay naturally (Schnitzer and Carson 2010). Lianas stems often sprout copiously after cutting (Putz 1984, Gerwing and Vidal 2002), and thus, we pruned liana sprouts every three months in the removal plots (methods follow Schnitzer and Carson 2010). We maintained a 10-m

buffer zone around the central  $60 \times 60$  m intensely sampled area for both the liana removal and control plots, which was sufficient to avoid effects of lianas from outside of the plot. We visually inspected the border of each plot to ensure that lianas were not entering the plots from outside the buffer zone.

We selected seven tree species that were abundant as sun-exposed canopy trees (100–200 mm trunk diameter) in six  $80 \times 80$  m plots (three removal and three control plots), which were part of the larger liana removal study. We then randomly selected two or three individuals per species from the available pool of species in each of the removal and control plots ( $N = 92$  trees total). The seven tree species represented six different families and varied 45% in wood density, ranging from 0.57 to 0.84 g/cm<sup>3</sup> (from Wright et al. 2010; Appendix A: Table A1). Wood density has been described as an intrinsic correlate of species-specific growth rate and as an index of shade tolerance; tree species with lower wood density tend to grow faster than those with higher wood density (Chave et al. 2006, van de Heijden et al. 2008). To account for the variability in liana abundance on the strength of liana competition at the individual tree level, we counted and measured the diameter of all liana stems in a 5 m diameter area surrounding each target tree prior to liana cutting (Ingwell et al. 2010). For each target tree, we also estimated liana infestation level in the crown, the position of the tree crown with respect to exposure to direct sunlight, and crown condition (follows Ingwell et al. 2010, Schnitzer and Carson 2010). We did not include liana species identity as a factor.

### *Meteorological variables and soil water content*

In all six plots, we recorded relative humidity and temperature every 10 min (Appendix B). We calculated water vapor pressure deficit (VPD) using relative humidity (RH) and temperature values (Jones 1992). We measured soil volumetric water content ( $\theta$ ; m<sup>3</sup>/m<sup>3</sup>) hourly by means of soil moisture sensors EC-5 (Decagon Devices, Pullman, Washington, USA) attached to a data logger Em 50 (Decagon Devices). One month prior to liana removal, we placed two loggers per plot, each with four soil moisture sensors at 10 cm ( $N = 48$ ) depth and one soil moisture sensor at 40 cm ( $N = 12$ ; Appendix E). We selected 10 cm soil depth because most of the fine roots in tropical forests are located within this soil depth (Powers et al. 2005). We used deep (40 cm depth) soil moisture sensors to measure the change in deep soil water as the dry season progressed. We used solar radiation and precipitation data collected at the closest meteorological station on Barro Colorado Island, 3 km away from the study plots (data provided by the Smithsonian Tropical Research Institute, Balboa, Panama; Appendix B).

### *Sap velocity*

We measured sap velocity as an estimate of tree transpiration and metabolic activity using the thermal dissipation method (Granier 1985). We manufactured





PLATE 1. Lianas in the forest understory on the Barro Colorado Nature Monument, Panama. Photo credit: Christian Ziegler.

temperature dissipation method (TDM) probes following Meinzer et al. (1999). On 1 April 2011, a week prior to the liana removal, we installed two sets of 20-mm probes in the trunk of each tree with north and south opposing locations in the trunk to avoid azimuthal temperature effects. We installed probes 1.5 m from the ground and inserted control and heated probes radially and 15 cm apart. We insulated probes with putty and an outer shield of reflective material. We recorded probe temperatures continuously and 10-min averages were stored in the data loggers. We calculated sap velocity from the temperature difference between the probes using an empirical relationship developed by Granier (1985). Data from each pair of probes per tree were averaged to a single value per tree.

We calculated daily average sap velocity values ( $v$ , mm/s) as the mean of sap velocity values recorded between 07:00 and 18:30 hours for each tree and day of study. We averaged normalized values per tree from consecutive sunny days before (precut) and after (postcut) liana removal, both during the dry and the wet period (follows Tobin et al. 2012). Our final sample size for sap velocity was reduced to six species and a total of 52 individual trees due to branch-falls and wildlife that broke cables and disconnected sensors (Appendix E).

We used precipitation and radiation data to verify dry- and wet-period conditions before and after the liana cutting. We classified the period as “dry” when

precipitation was absent for at least seven consecutive days during the late dry season, with relatively high solar radiation levels and VPD (Appendix C). We classified the period as “wet” when precipitation occurred for at least seven consecutive days during the wet season. The period when precipitation started after the dry period but was intermittent was considered as “intermediate.” We collected sap velocity measurements for a period of 60 days from 8 April 2011 until 8 June 2011. We calculated the relative change in sap velocity for each tree as the natural log of postcut sap velocity divided by precut sap velocity from each period (dry, intermediate, and wet):  $\ln(\text{postcut } v / \text{precut } v)$ . We calculated precut sap flow for each tree as the mean sap flow following seven days without precipitation prior to liana cutting.

#### *Tree growth*

We measured annual tree growth using plastic dendrometer bands, which we installed around each target tree trunk 1.30 cm above ground or above buttresses if present. We installed dendrometers three months before liana cutting to allow the dendrometer bands to settle on the trunk (Keeland and Sharitz 1993). We measured the dendrometer bands immediately before liana cutting and then again one year following liana cutting, in March 2012.

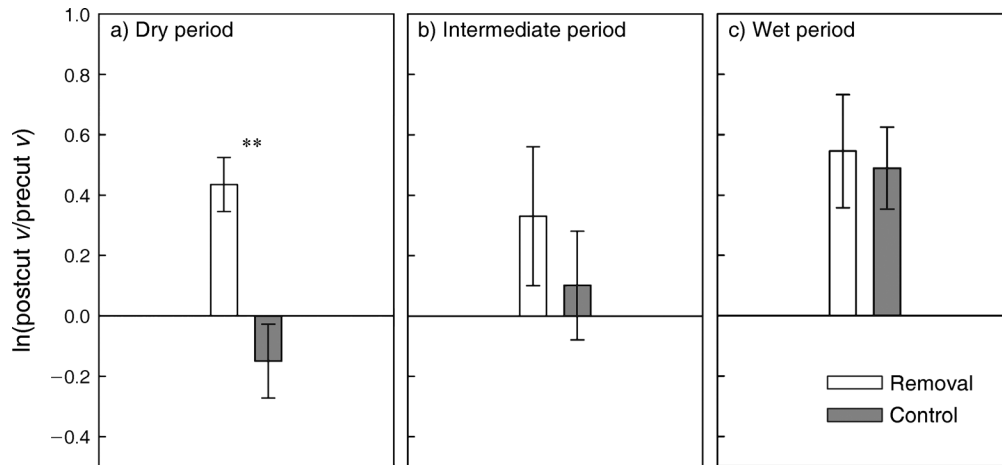


FIG. 1. Mean change in daily sap velocity ( $v$ , mm/s) in trees after liana removal in removal (white bars) and control plots (gray bars) on Gigante Peninsula in Barro Colorado National Monument, Panama, during three periods (dry, intermediate, and wet). Relative change in sap velocity was calculated as the natural log of postcut sap velocity divided by precut sap velocity:  $\ln(\text{postcut } v / \text{precut } v)$ . Data are presented on a natural logarithmic scale. Error bars represent  $\pm$ SE. Asterisks denote significant differences between treatments (ANCOVA, \*\*  $P < 0.01$ ). Sample sizes for each period and treatment were: dry period, removal  $N = 32$  and control  $N = 16$ ; intermediate period, removal  $N = 31$  and control  $N = 14$ ; wet period, removal  $N = 28$  and control  $N = 16$ .

#### Statistical analyses

We tested whether there were significant differences in VPD, soil volumetric water content, and sap velocity changes between seasons and treatments using a repeated-measures ANOVA with treatment (liana removal vs. control) as the between subject effect and season (dry, intermediate, and wet) as the within-subject effect. We used a Mauchly's test for the sap velocity data to test for sphericity, and, because it was significant ( $P = 0.038$ ), we applied the Greenhouse-Geisser correction. We tested whether lianas reduced tree sap velocity and annual growth, and whether the response to lianas varied among tree species, using an ANCOVA with treatment and species as fixed factors. We log-transformed growth data to meet assumptions of normality. We performed a principal component analyses (PCA) on the following factors: (1) the number of lianas surrounding each tree, (2) level of liana infestation in tree canopy, (3) tree canopy condition, and (4) tree diameter, reducing them to a single factor that we used as a continuous covariate in the ANCOVA. The first axis of the PCA explained 38% of the variation in the covariates. We analyzed the effect of liana removal on tree sap velocity during the dry, intermediate, and wet periods on soil volumetric water content using a one-way ANOVA with treatment as a fixed factor. We performed the statistical analyses using R package 2.10 (R Development Core Team 2012) and Statistica 11 (StatSoft 2012).

#### RESULTS

Liana competition substantially reduced tree physiological performance, leading to an increase in sap velocity in removal trees during the dry season. Tree sap velocity increased 60% following liana removal

during the dry season, while tree sap velocity in plots with lianas present decreased 10% relative to the precut values during this period ( $F_{1,26} = 7.16$ ,  $P < 0.01$ , covariate  $F_{1,26} = 0.002$ ,  $P = 0.95$ ; Fig. 1a). The effect of lianas on sap velocity varied significantly with season (repeated-measures ANOVA, season  $\times$  treatment interaction,  $F_{1,98,70} = 5.47$ ,  $P < 0.01$ ). During the intermediate period, when there was some rain, trees without lianas tended to have higher sap velocity relative to control trees, but this pattern was not significant (Fig. 1b). During the wet season, the difference in sap velocity between trees without lianas and trees in the control disappeared (Fig. 1c). Tree basal growth was 25% higher in the liana removal treatment compared to the control trees one year after liana cutting ( $F_{1,55} = 7.43$ ,  $P < 0.001$ , covariate  $F_{1,55} = 0.011$ ,  $P = 0.91$ ), confirming that the dry- and intermediate-season sap flow differences were associated with greater tree growth.

Lianas had a negative effect on all tree species in the study. Although some tree species responded more strongly than others to liana removal, the species  $\times$  treatment interaction was not significant for sap velocity effect during the dry season ( $F_{5,26} = 1.76$ ,  $P = 0.15$ ; Appendix D). Likewise, one year after cutting, all tree species had grown more after liana removal than in control plots, and growth did not vary significantly with tree species identity ( $F_{5,55} = 1.04$ ,  $P = 0.40$ ; Fig. 2).

Shallow soil moisture (0–10 cm) decreased during the dry season and increased during the intermediate and wet periods, after the first rains in both removal and control plots (repeated-measures ANOVA, season,  $F_{2,76} = 367.1$ ,  $P < 0.001$ ). We did not detect a significant effect of liana removal on mean soil volumetric water content at 10 cm depth during any season (repeated-measures ANOVA, season  $\times$  treatment interaction,  $F_{2,76} = 0.38$ ,  $P$



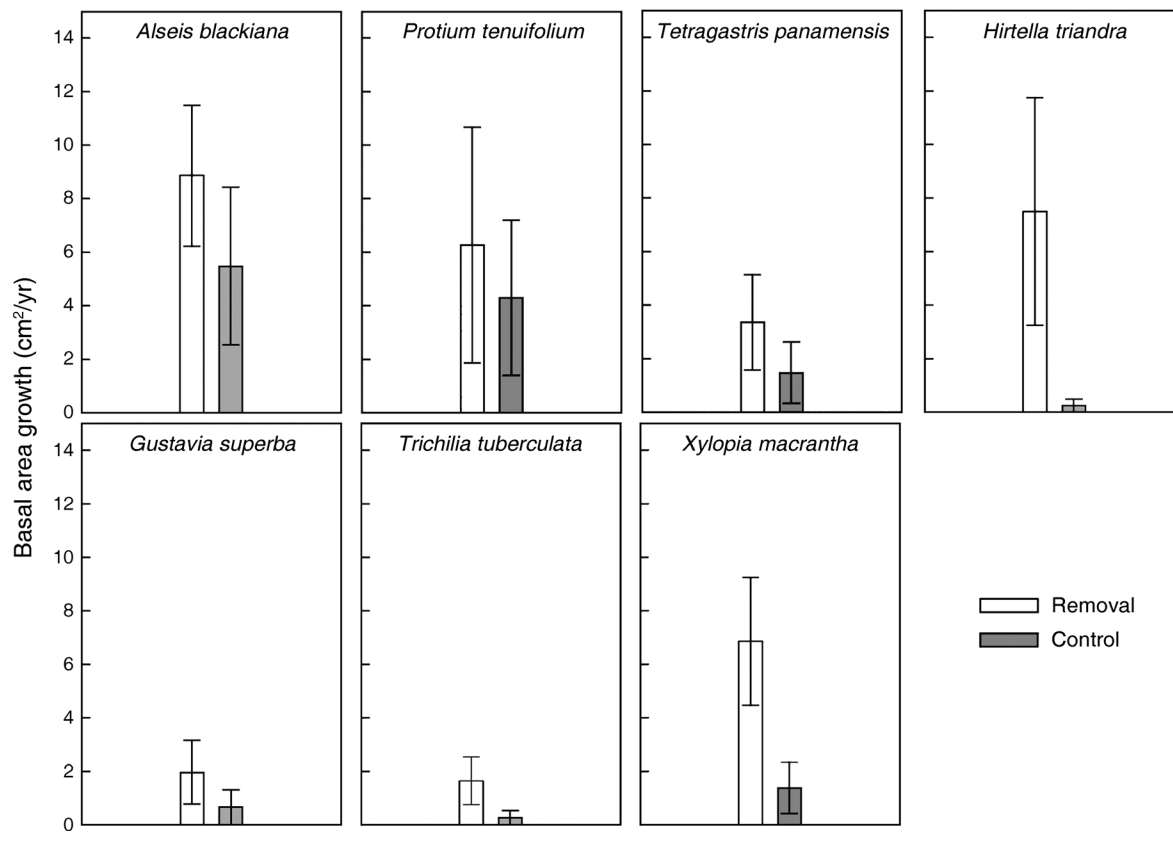


FIG. 2. Mean tree basal area increment growth per species in removal (white bars) and control plots (gray bars) one year following liana cutting. Error bars represent  $\pm$ SE. Panels are ordered by species with highest to lowest wood density. There was no significant species  $\times$  treatment interaction (ANCOVA), indicating that the tree species did not differ in their response to liana removal. Sample sizes in the removal and in the control plots were  $N = 63$  and  $N = 42$ , respectively.

= 0.68) or at the 40 cm depth (repeated-measures ANOVA,  $F_{2,16} = 0.068$ ,  $P = 0.93$ ), although an analyses of all 16 plots in the larger experiment found significantly higher dry-season soil moisture values at 10 cm in the liana removal plots following cutting (J. P. Reid et al., *unpublished manuscript*). Vapor pressure deficit (VPD) also did not differ significantly in the control and removal plots (repeated-measures ANOVA,  $F_{44,132} = 0.52$ ,  $P = 0.99$ ; Appendix C).

#### DISCUSSION

Our experimental results demonstrate that lianas reduce tree physiological performance and growth. Tree sap velocity increased immediately after liana removal compared to control plots, confirming that lianas compete intensely with trees. The effect of liana removal on tree sap velocity was significant only during the dry season, with the intensity of liana competition apparently diminishing with increasing rainfall. These findings demonstrate that liana competitive effects are strong, seasonal, and that lianas have a much stronger competitive effect during periods of water stress.

Our findings are consistent with other experimental studies that show that lianas reduce tree performance (e.g., Grauel and Putz 2004, Schnitzer et al. 2005). However, previous studies used only tree growth integrated over years to determine the negative effect of lianas on trees (e.g., Grauel and Putz 2004, Schnitzer and Carson 2010). Those studies, with the exception of Tobin et al. (2012), did not examine the seasonal aspect of liana competition. By examining tree sap velocity seasonally, we were able to show that liana competition was strongest during seasonal drought, and that it diminished with increasing rainfall. This finding implies that, as lianas continue to increase in tropical forests (Schnitzer and Bongers 2011), they will have a stronger competitive effect during seasonal drought.

In a separate study on Gigante Peninsula, G. M. F. van der Heijden and S. A. Schnitzer (*unpublished data*) have been following the precise long-term seasonal growth of multiple liana and tree species using dendrometer bands and found that liana growth rates are higher during the dry season than the wet season, indicating that lianas have the capacity to compete with trees during the dry season. Tobin et al. (2012) also

found a significant increase in target-tree sap velocity during the dry season compared to control trees where lianas were present. The competitive effect of lianas was diminished and was not significant during the wet season (Tobin et al. 2012). Several other studies have also reported that belowground competition from lianas, apparently for water, significantly limited tree growth (Dillenberg et al. 1993, Pérez-Salicrup and Barker 2000, Schnitzer et al. 2005, Toledo-Aceves and Swaine 2008). Consequently, belowground interactions appear to be an important component of liana–tree competition.

Previous studies have demonstrated that many tree species were largely inactive during seasonal droughts, presumably due to their sensitivity to water stress, while lianas remained active (e.g., Schnitzer 2005). However, the strong increase of tree sap flow with liana removal in the dry season found in this study suggests that liana competition for water and low water availability may combine to limit tree growth during periods of drought. We did not detect a change in soil moisture after liana cutting, possibly because trees quickly depleted the soil moisture that was available following liana cutting, thus resulting in no net change in shallow-soil moisture. However, in the larger study, J. P. Reid et al. (*unpublished manuscript*) found that shallow (10-cm) soil moisture in the liana removal plots dried more slowly than in the controls during the study period, suggesting that the absence of lianas resulted in more water availability for tree growth.

Aboveground competition also may be occurring between lianas and trees. After liana removal, trees receive more light, thus increasing tree transpiration and ultimately, growth. Understory light levels in the liana removal plots increased by 15% six weeks and 20% one year after liana cutting (M. E. Rodriguez et al., *unpublished data*), which may have stimulated tree growth. By contrast, in seasonal tropical forests, where precipitation is scarce or absent for months, belowground competition may become an important limiting factor for tree growth and survival during the dry season (e.g., Schnitzer et al. 2005, Toledo-Aceves and Swaine 2008). Indeed, our data, along with previous studies (Dillenberg et al. 1993, Pérez-Salicrup and Barker 2000, Schnitzer et al. 2005, Toledo-Aceves and Swaine 2008, Tobin et al. 2012) indicate that belowground competition predominates between lianas and trees.

Our experimental design does not allow us to discriminate between water and nutrients as the more limiting resource for tree growth. Nonetheless, trees in both the control and liana removal plots increased transpiration with the onset of the first rains and increase in soil moisture, suggesting that water was an important limiting factor. Lianas may have well-developed root systems that give them access to water and nutrients during dry periods in seasonal forests, thus allowing them to compete intensely for belowground resources (Restom and Nepstad 2004, Andrade et al. 2005, Schnitzer 2005, Toledo-Aceves and Swaine 2008).

Our data indicate that liana competition on trees was strongest during the dry season, thus demonstrating that the intensity of liana competition on trees varies seasonally. Consequently, the ability of lianas to grow during seasonal drought appears to result in strong dry-season competition and limits tree growth.

Our study differed from that of Tobin et al. (2012) because we included more tree individuals and species, and we replicated at the species level, thus allowing us to test whether the lianas effect varies with tree species identity and woody density. While lianas have been found to compete less with select pioneer species, such as *Cecropia* spp. (Clark and Clark 1990, Ingwell et al. 2010), we found that lianas competed, in varying degrees, across a range of tree species-specific wood densities that varied by 45%. Although there was variation among tree species in their response to lianas, there was no significant treatment  $\times$  species interaction for diameter growth or for sap velocity. Our replication for diameter growth was greater than for sap flow (92 vs. 52 total individuals), and should have been sufficient to detect a strong species  $\times$  treatment interaction had one been present. If lianas compete with most tree species in a similar manner, then ongoing increases in liana abundance will be detrimental to most tropical trees, regardless of their identity.

#### ACKNOWLEDGMENTS

Financial support was provided by NSF-DEB 0845071 and NSF-DEB 1019436 to S. A. Schnitzer, NSF DEB-1019441 to J. S. Powers, and a Research Growth Initiative award from the University of Wisconsin-Milwaukee to S. A. Schnitzer. Logistical support was provided by the Smithsonian Tropical Research Institute.

#### LITERATURE CITED

- Andrade, J. L., F. C. Meinzer, G. Goldstein, and S. A. Schnitzer. 2005. Water uptake and transport in lianas and co-occurring trees of a seasonally dry tropical forest. *Trees* 19: 282–289.
- Cai, Z.-Q., S. A. Schnitzer, and F. Bongers. 2009. Seasonal differences in leaf-level physiology give lianas a competitive advantage over trees in a tropical seasonal forest. *Oecologia* 161:25–33.
- Chave, J., H. C. Muller-Landau, T. R. Baker, T. A. Easdale, H. ter Steege, and C. O. Webb. 2006. Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecological Applications* 16:2356–2367.
- Clark, D. B., and D. A. Clark. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology* 6:321–331.
- Condit, R. 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plants. Springer-Verlag, Berlin, Germany.
- Dillenberg, L. R., D. F. Whigham, A. H. Teramura, and I. N. Forseth. 1993. Effects of vine competition on availability of light, water, and nitrogen to a tree host (*Liquidambar styraciflua*). *American Journal of Botany* 80:244–252.
- Gervig, J. J., et al. 2006. A standard protocol for liana censuses. *Biotropica* 38:256–261.
- Gervig, J. J., and E. Vidal. 2002. Changes in liana abundance and species diversity eight years after liana cutting and

- logging in an eastern Amazonian forest. *Conservation Biology* 16:544–548.
- Granier, A. 1985. Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Annales des Sciences Forestières* 42:193–200.
- Grauel, W. T., and F. E. Putz. 2004. Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. *Forest Ecology and Management* 190:99–108.
- Ingwell, L. L., J. S. Wright, K. K. Becklund, S. P. Hubbell, and S. A. Schnitzer. 2010. The impact of lianas on 10 years of tree growth and mortality on Barro Colorado Island, Panama. *Journal of Ecology* 98:879–887.
- Jones, H. G. 1992. Plants and microclimate. Cambridge University Press, Cambridge, UK.
- Keeland, B. D., and R. R. Sharitz. 1993. Accuracy of tree growth measurements using dendrometer bands. *Canadian Journal of Forest Research* 23:2454–2457.
- Leigh, E. G. 1999. Tropical forest ecology. Oxford University Press, New York, New York, USA.
- Meinzer, F., J. Andrade, G. Goldstein, and N. Holbrook. 1999. Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* 121:293–301.
- Pérez-Salicrup, D. R. 2001. Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia. *Ecology* 82:389–396.
- Pérez-Salicrup, D. R., and M. G. Barker. 2000. Effect of liana cutting on water potential and growth of adult *Senna multijuga* (Caesalpinioideae) trees in a Bolivian tropical forest. *Oecologia* 124:469–475.
- Pérez-Salicrup, D. R., V. L. Sork, and F. E. Putz. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. *Biotropica* 33:34–47.
- Powers, J. S., K. K. Treseder, and M. T. Lerdau. 2005. Fine roots, arbuscular mycorrhizal hyphae and soil nutrients in four neotropical rain forests: patterns across large geographic distances. *New Phytologist* 165:913–921.
- Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Restom, T. G., and D. C. Nepstad. 2004. Seedling growth dynamics of a deeply rooting liana in a secondary forest in eastern Amazonia. *Forest Ecology and Management* 190: 109–118.
- Sánchez-Azofeifa, G. A., M. Kalacska, M. M. D. Espírito-Santo, G. W. Fernandes, and S. A. Schnitzer. 2009. Tropical dry forest succession and the contribution of lianas to wood area index (WAI). *Forest Ecology and Management* 258: 941–948.
- Schnitzer, S. A. 2005. A mechanistic explanation for the global patterns of liana abundance and distribution. *American Naturalist* 166:262–276.
- Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17: 223–230.
- Schnitzer, S. A., and F. Bongers. 2011. Increasing liana abundance and biomass in tropical forests: emerging patterns and putative mechanisms. *Ecology Letters* 14:397–406.
- Schnitzer, S. A., F. Bongers, and S. J. Wright. 2011. Community and ecosystem ramifications of increasing lianas in neotropical forests. *Plant Signaling and Behavior* 6:598–600.
- Schnitzer, S. A., and W. P. Carson. 2010. Lianas suppress tree regeneration and diversity in treefall gaps. *Ecology Letters* 13:849–857.
- Schnitzer, S. A., M. Kuzee, and F. Bongers. 2005. Disentangling above- and belowground competition between lianas and trees in a tropical forest. *Journal of Ecology* 93:1115–1125.
- Schnitzer, S. A., S. Rutishauser, and S. Aguilar. 2008. Supplemental protocol for liana censuses. *Forest Ecology and Management* 255:1044–1049.
- StatSoft. 2012. Statistica version 11. StatSoft, Tulsa, Oklahoma, USA.
- Tobin, M. F., A. J. Wright, S. A. Mangan, and S. A. Schnitzer. 2012. Lianas have a greater competitive effect than trees of similar biomass on tropical canopy trees. *Ecosphere* 3:20.
- Toledo-Aceves, T., and M. D. Swaine, M. D. 2008. Above- and below-ground competition between the liana *Acacia kame-runensis* and tree seedlings in contrasting light environments. *Plant Ecology* 196:233–244.
- van der Heijden, G. M. F., J. R. Healey, and O. L. Phillips. 2008. Infestation of trees by lianas in a tropical forest in Amazonian Peru. *Journal of Vegetation Science* 19:747–756.
- van der Heijden, G. M. F., S. A. Schnitzer, J. S. Powers, and O. L. Phillips. 2013. Liana impacts on carbon cycling, storage and sequestration in tropical forests. *Biotropica* 45:682–692.
- Wright, S. J., et al. 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91:3664–3674.

## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/14-1002.1.sm>